

Commentary: do we have a consistent terminology for species diversity? Yes, if we choose to use it

Hanna Tuomisto

Received: 18 June 2011 / Accepted: 1 September 2011 / Published online: 27 September 2011
© Springer-Verlag 2011

Abstract Meaningful quantification of species diversity requires that both ‘species’ and ‘diversity’ are unambiguously defined. Rigorous rules of nomenclature exist to ensure that each species has a single unique name, but the naming of concepts is much more variable. As a consequence, ‘diversity’ has been defined in so many different ways that its ability to transfer accurate information has been compromised. This problem can be solved by defining ‘diversity’ as the effective number of species (or other types of interest), and using the term ‘true diversity’ to specify that this narrow concept is being used (analogously to using the term ‘true bugs’ when adhering to a narrow circumscription of ‘bugs’). Other measures related to diversity (such as entropies and probabilities) continue to be useful, but they represent different phenomena and should therefore be referred to by different names. Total species diversity in a dataset can be partitioned into two components in several different ways. The components of a specific multiplicative partitioning can be called true alpha diversity and true beta diversity. When the partitioning is done in some other way, the resulting components are different and should be called by other names. For example, the beta component of additive partitioning does not equal true beta diversity, but can logically be called species turnover. All the phenomena that have been called ‘beta diversity’ in the ecological literature have also been called by alternative unique names. Consequently, a consistent

terminology is already available; only a general agreement to use it is lacking.

Keywords Alpha diversity · Beta diversity · Gamma diversity · Diversity partitioning · Species turnover

The need for consistent terminology

Quantifying taxonomic diversity requires information on the number of species (or other taxa) and on the evenness of their abundances. Any quantitative estimate of taxon diversity is only meaningful if the ‘one taxon–one name’ principle is adhered to, because otherwise tallying taxon names does not help in establishing how many taxa have been encountered. The importance of ensuring that each taxon has a unique and unambiguous name is so universally acknowledged that considerable effort has been invested in establishing rigorous rules to guide the naming of organisms (such as the International Code of Botanical Nomenclature). When it is found that one name has been applied to several different taxa (and the name refers to a polyphyletic group), the rules dictate that only one taxon can keep the original name, and the other taxa must be given new names.

Quantifying diversity also requires that it is known to which phenomenon ‘diversity’ refers, as otherwise the wrong thing might be measured. And here lies a difficulty: no International Code of Conceptual Nomenclature exists to dictate consistent naming of concepts, so ecologists with different preferences and interests have defined ‘diversity’ in different ways. As a consequence, two ecologists may be quantifying entirely different (conceptually “polyphyletic”) phenomena although both are focusing on ‘species diversity’.

Communicated by Scott Collins.

H. Tuomisto (✉)
Department of Biology, University of Turku,
20014 Turku, Finland
e-mail: hanna.tuomisto@utu.fi

Hurlbert (1971) phrased the problem succinctly: “The term ‘species diversity’ has been defined in such various and disparate ways that it now conveys no information other than ‘something to do with community structure’; species diversity has become a nonconcept”. Since then, several researchers have attempted to restore information value to the term by recommending that ‘species diversity’ be only used to refer to the effective number of species (e.g., Hill 1973; Routledge 1979; Jost 2006, 2007, 2009; Tuomisto 2010a, b, c; Jurasinski and Koch 2011; Moreno and Rodríguez 2011). To clarify the terminology, Jost (2006, 2007) proposed using the term ‘true diversity’ to make it explicit that this narrow definition of diversity is being used. This is one step towards a consistent terminology for species diversity, which can only be reached if we do as the taxonomists have done and adhere to the ‘one phenomenon–one name’ principle.

The meaning of ‘true’ in ‘true diversity’

The term ‘true diversity’ has triggered surprisingly strong negative reactions (Hoffmann and Hoffmann 2008; Anderson et al. 2011; Gorelick 2011). Apparently, there is a feeling that since the common usage of the word ‘diversity’ is very broad, we must allow its use in an equally broad sense in the scientific context. The word ‘true’ has also been (wrongly) interpreted to imply that what is ‘true’ is also ‘best’, and that there must be something wrong with the measures not called ‘true’ so these should be abandoned. However, several examples exist of other words that are also used in a broader (and imprecise) sense in everyday language, and in a stricter (logically more coherent) sense in scientific contexts.

For example, the word ‘bug’ can refer to a pathogenic microorganism such as a bacterium, any insect-like animal, or insects of the order Heteroptera, also known as ‘true bugs’. Since ‘bug’ can refer to many critters that zoologists know to be unrelated, in a scientific context the specifier ‘true’ is added to make sure it is understood that insects of the order Heteroptera are meant, rather than bacteria, beetles or millipedes. The word ‘true’ is simply used to specify that a monophyletic taxon within the polyphyletic assemblage ‘bugs’ is being referred to, and it does not imply any opinion on the ecological importance or scientific interest of true bugs in relation to bacteria, beetles or anything else. Of course, the scientific name of the group, Heteroptera, could be used to convey the same information as ‘true bugs’, but in some situations it is preferable to use a term that is more familiar to non-entomologists. Other alternatives either sound silly, like ‘bugs *sensu stricto*’, or are more cumbersome to use, like ‘bugs in the narrow sense’.

The use of the word ‘true’ to specify ‘*sensu stricto*’ is not restricted to bugs, either. A group of birds is known as ‘true tits’, and a group of mammals is known as ‘true seals’. In plant morphology, ‘true leaves’, ‘true roots’ and ‘true veins’ each have specific characteristics that distinguish them from other superficially similar plant structures, such as phylloclades, rhizoids and false veins, respectively.

The use of the word ‘true’ in ‘true diversity’ is no different from its use in ‘true bugs’ or ‘true leaves’. In common use, the word ‘diversity’ can be used very broadly, for example to refer to the state or fact of being diverse, difference, unlikeness, or multiformity. However, these phenomena form a conceptually heterogeneous bunch. ‘Difference’ and ‘unlikeness’ involve the degree of difference between two objects in some characteristic, and they can logically be quantified by subtracting the value of the relevant variable in one object from its value in the other. In contrast, ‘multiformity’ is more naturally quantified by counting how many different forms there are, which involves classifying the objects into non-overlapping groups on the basis of some qualitative or quantitative criterion.

When the word ‘diversity’ is used on its own in the ecological literature, the purpose is usually to convey the idea of multiformity. Hill (1973) discussed the concept of diversity from this starting point, and concluded that ‘species diversity’ is best thought of as the effective number of species. Jost (2006, 2007) then proposed the term ‘true diversity’ to explicitly specify that this narrow, logically coherent (“monophyletic”) definition of diversity is being used, instead of the broader definition that includes all kinds of conceptually different (“polyphyletic”) phenomena. I have adopted Jost’s terminology, because it makes practical sense (Tuomisto 2010a, b, c).

The term ‘true diversity’ is simply meant to facilitate accurate communication, and it should not be interpreted as an evaluation of the usefulness or scientific value of the phenomena involved (as is done by Hoffmann and Hoffmann 2008; Anderson et al. 2011; Gorelick 2011). The situation is exactly the same as in the case of ‘true bugs’. Zoological texts would become very confusing if researchers insisted on calling all pathogenic microorganisms and insect-like animals ‘bugs’, and it would seem very odd to reject the term ‘true bugs’ on the grounds that it “demeans other kinds of bugs without justification and without a specific biological question to be answered” (as Gorelick 2011 wrote of true diversity). Both in the case of bugs and in the case of diversity, ‘true’ is used as a synonym of “in the narrow sense”, not as a synonym of “the only one worth considering”. Indeed, taxonomists show that they recognise something as worthy of distinction by giving it a name of its own, and the same principle can be applied to concepts.

The meaning of ‘diversity’

It is not uncommon for ecologists to treat the value of any diversity index as if it equaled ‘diversity’. However, different diversity indices correspond to conceptually very different things (Hill 1973; Jost 2006, 2007, 2009; Tuomisto 2010a; Moreno and Rodríguez 2011). True diversity is an effective number of types (such as species). It is notated qD , where the parameter q can be varied to change the weight given to abundant versus rare species. Richness does not take abundance information into account at all, and is hence an actual rather than effective number of types. In contrast, the Shannon index [$=\log({}^1D)$] is a measure of uncertainty (entropy) and the Gini–Simpson index ($=1 - 1/{}^2D$) is a measure of probability; neither one represents a count of types.

Hill (1973) defined diversity (=the effective number of types) as the inverse of mean proportional species abundance, with the mean referring to the weighted generalized mean with exponent $q - 1$ (Fig. 1). There is no mathematical reason to declare that only some values of q are allowed when calculating a generalized mean, so any value of q gives a valid mean and hence a valid true diversity (although in practical applications only $q \geq 0$ are likely to be useful). For example, the harmonic mean (which corresponds to $q = 0$) takes a smaller value (i.e. is closer to

the proportional abundance of the rarest species) than the geometric mean ($q = 1$), and the arithmetic mean ($q = 2$) takes a larger value still (i.e. is closer to the proportional abundance of the most abundant species; Fig. 1). For this reason, any given value of true diversity is informative only when the mean used when calculating it is known.

Because of the free parameter q in qD , infinitely many true diversity values can be calculated for any given dataset. Gorelick (2011) seems to find this a problem, and argues that the word ‘true’ implies that only one diversity index can be called ‘true diversity’. However, this is like arguing that only one species can be called ‘true bugs’. In my opinion, the important thing is that all the included measures (or taxa) form a logically coherent (or monophyletic) group.

Although both the Shannon entropy and the Gini–Simpson probability can be expressed as simple transformations of true diversity, they are still transformations and therefore each represents a different phenomenon. Using the terms ‘entropy’, ‘probability’ and ‘true diversity’ makes it explicit at once which of the three is meant; using the generic term ‘diversity’ for all three easily leads to confusing them.

Analogously, the circumference, surface area and volume of a sphere are simple transformations of each other, but each still represents a different phenomenon and should

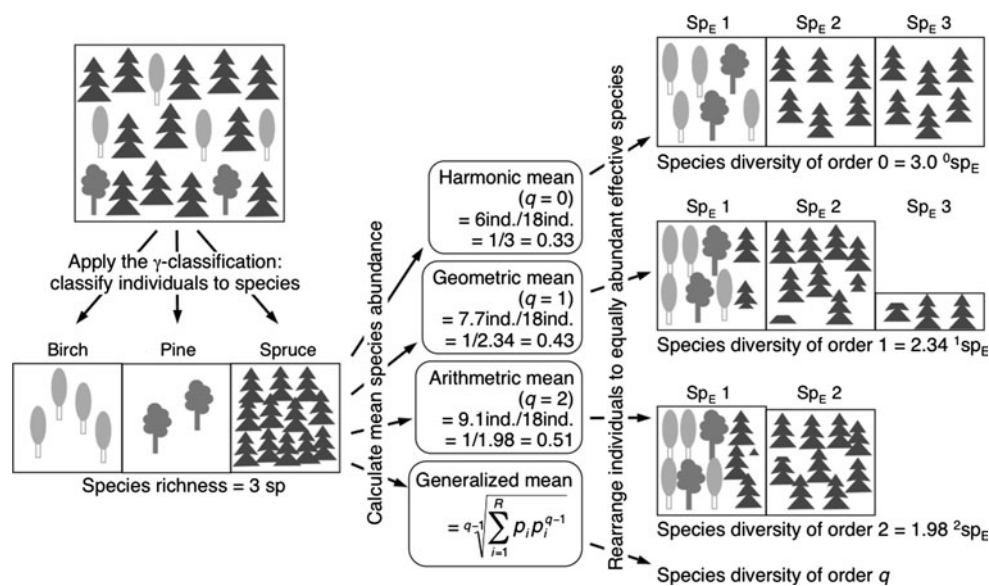


Fig. 1 The calculation of species richness and species diversity in a small dataset consisting of a single tree plot. Species richness is the number of slots needed (the set to the left) to place all individuals into a slot with an appropriate species name. Species diversity is the number of slots needed (the sets to the right) to place all individuals into a slot such that each slot receives as many individuals (or as large a proportion of all individuals) as the slots of named species have on average. The measure of ‘average’ here is the weighted generalized mean with exponent $q - 1$. This can be calculated by first taking the

weighted mean of the absolute species abundances ($=6, 7.7$ and 9.1 individuals for $q = 0, 1$ and 2 , respectively) and then dividing this by total abundance (18 ind.). Equally well, one can calculate the weighted mean of the proportional abundances directly (as shown in the equation of the generalized mean; R is the number of actual named species and p_i is the proportional abundance of the i th species). Species diversity qD equals the inverse of mean p_i , and it is the effective number of species (=the number of equally-abundant species that would give the observed mean species abundance)

be called by a different name in order to avoid confusing them. Gorelick (2011) seems to argue that the Banach–Tarski paradox makes the concept of volume undefinable. However, the paradox only concerns the quantification of volume when duplicating a theoretical sphere, and it is not relevant either when measuring the volume of physical objects or when deciding whether volume, surface area and circumference represent different concepts or the same concept. When dealing with real-world spheres, we can therefore continue to treat their volumes as conceptually distinct from their surface areas and circumferences, and all three properties as exactly calculable if the radius of the sphere and the value of π are known. Similarly, we can treat (true) diversity as distinct from (Shannon) entropy and (Gini–Simpson) probability, and all three properties of a dataset as exactly calculable if the proportional abundances of the species are known.

Gorelick (2011) wrote: “The Hill indices do not account for either geographic or phylogenetic structure, therefore, when either matter, it would be wise to invoke a different measure of diversity”. I would completely agree with this sentence if the last two words were deleted. The fundamental disagreement that Gorelick and I have is not whether the choice of measure should depend upon the ecological question being asked—we agree that it should—but whether the chosen measure should always be called ‘diversity’. I think this should only be done if the measure corresponds to true diversity, because otherwise the term ‘diversity’ is reduced to meaning “whichever phenomenon happens to be of interest in this particular case”. If a word can mean different things depending on the context, its use leads to misunderstandings and hence its value in transferring accurate information is lost.

Is ‘beta diversity’ a diversity?

Another issue that seems to be causing divergence of opinion is what the function of specifier words attached to a noun is. In scientific taxonomy, the specifier narrows down the meaning of the main word. For example, the genus *Malus* corresponds to the apples, of which the true (cultivated) apple belongs to *Malus domestica* and the crab apple to *M. sylvestris*, both of which are species of *Malus*. Similarly in the diversity literature, ‘species diversity’ and ‘gamma diversity’ refer to what one would normally call ‘diversity’, and each specifier narrows the term down to a specific kind of diversity.

In everyday usage, however, specifiers can also indicate that what is meant is not really what the noun implies, but something else. Many kinds of plants are colloquially called “apples”, although they do not belong to the genus *Malus* or even to the family Rosaceae, such as mayapples

(Berberidaceae), custard apples (Annonaceae) and pine-apples (Bromeliaceae). In some languages, oranges (Rutaceae) and potatoes (Solanaceae) are also called apples (Chinese apples and ground apples, respectively).

In the diversity literature, the term ‘beta diversity’ has been used to refer to a wide range of unrelated phenomena, such as various kinds of difference, dispersion, gradient length and rate of change (reviewed in Jurasinski et al. 2009 and Tuomisto 2010a, b). Most of these phenomena would not be called ‘diversity’ at all if the noun were not preceded by ‘beta’, which undermines the logical coherence of the terminology. In fact, the diversity situation is much worse than the apple situation: ‘beta diversity’ is only one term, but it is being used to refer to about 30 different phenomena. This is like using the name *Malus domestica* for any plant whose colloquial name refers to apples. To clarify the relationships between the different phenomena that have been lumped under the name ‘beta diversity’, I have suggested using alternative descriptive names for them (Tuomisto 2010a, b, c).

Anderson et al. (2011) drafted a roadmap to assist in navigating the multiple meanings of beta diversity. From the point of view of the practising ecologist, their roadmap has two serious shortcomings: it has all landmarks labeled by the same name, and it fails to clearly indicate what kind of structure each landmark represents (see also Moreno and Rodríguez 2011). Imagine trying to navigate with instructions like “follow Station Road until it crosses Station Road, then turn right and continue until you reach Station Road” when not only roads but also bridges, railways and rivers are labeled ‘Station Road’ on the map.

The term ‘Station Road’ implies that the structure being referred to is a road, and suggests that it passes by a station. Similarly, the term ‘beta diversity’ implies that the phenomenon being referred to is a diversity, and suggests that it is related to other diversities identified by a Greek letter, such as alpha and gamma diversity. Using the term ‘beta diversity’ to refer to phenomena that are not themselves diversities and are not related to alpha and gamma diversity is just as counterintuitive and misleading as using the name Station Road for a river in the wilderness, or the name *Malus domestica* for a wild plant that does not belong to the genus *Malus*.

If it is found out that the same name has been given to unrelated taxa, the nomenclature code dictates which taxon is allowed to keep that name, and which are to be given new names. The names also have to make hierarchical sense, such that every species labeled with the same genus name can be assumed to belong to the same genus. Diversity research could be made much more rigorous than it is at present if it were required to follow equally logical naming principles. Then only one phenomenon—which must itself be a diversity—would be called ‘beta diversity’,

and all other phenomena would be referred to by other names.

Even the critics of the term ‘true diversity’ admit that it is important to be explicit about which phenomenon one is referring to when discussing (beta) diversity (Anderson et al. 2011; Gorelick 2011). It remains unclear how researchers can possibly be explicit if the ‘one phenomenon–one name’ principle is rejected, and all the different phenomena that can be of interest when discussing community heterogeneity are called beta diversity. It is very difficult to avoid comparing apples and oranges if both are called *Malus domestica* in the literature.

Imagine that a cookbook declared in its introduction that it will use the term ‘apple’ in the broad sense to refer not only to true apples but also to pears, oranges, bananas, strawberries, potatoes, turnips and cabbages. Who would want to base their cooking on recipes that are ambiguous as to whether a dish is supposed to contain cabbages or strawberries? It is difficult to understand why similar ambiguity in the terminology related to diversity continues to be tolerated in a scientific discipline.

The logic of diversity partitioning

When Whittaker (1960) coined the term ‘beta diversity’, his intention was to understand the species diversity in a landscape (gamma diversity) as the combined result of two different phenomena, the species diversity at a more local scale (alpha diversity), and the compositional heterogeneity among localities (beta diversity). He explored several approaches to quantifying compositional heterogeneity, each one of which is useful for targeting some ecological questions. However, each approach quantifies a different phenomenon, and it is unfortunate that Whittaker referred to all of them as ‘beta diversity’. This prodded the term towards becoming a nonconcept that currently conveys even less information than does ‘species diversity’.

Whittaker (1960) did write that a simple way to achieve his purpose is by defining $\beta = \gamma/\alpha$. This is the only one of Whittaker’s definitions of beta diversity that is itself a diversity, which I think is sufficient justification to allow it to keep the name ‘beta diversity’, and to rename all the other definitions. Of the three variables in the equation, γ is the least ambiguous, as it is simply the total species diversity in the dataset of interest (Fig. 1). Unfortunately, Whittaker used different definitions of ‘diversity’ in parallel, so in his texts γ can refer either to a true diversity, to the raw value of a diversity index, or to species richness. His definition of alpha diversity was even less precise. The first mention of ‘alpha diversity’ in Whittaker (1960) is accompanied by the explanation “The richness in species

of a particular stand or community” (p. 320). The second explanation (p. 321) reads “Fisher alpha measurements for average numbers of tree species and individuals”. A third definition is given in Whittaker (1972: p. 214), where it is said that “When a set of samples are taken... beta differentiation for these samples may be expressed by the ratio of the total number of species represented in the samples to the mean number per sample”.

The third definition of α is the only one that Whittaker backed up with an explicit equation: he specified (Whittaker 1972: p. 232) that $\beta = \gamma/\alpha$ can be appropriately measured with S_c/\bar{S} . Here S_c is the total number of species in the composite set of samples (subunits) and \bar{S} is the mean number of species in the individual samples (subunits). If α were defined as the species diversity of a single subunit, then each dataset would have as many α values, and as many β values, as it has subunits (see Tuomisto 2010b and Jurasinski and Koch 2011 for a discussion on the importance of calculating alpha and gamma diversity from the same data). Although partitioning gamma diversity in all these ways is entirely possible, Whittaker’s purpose was to obtain a single partitioning that describes the dataset with one α value and one β value, and for this purpose the most appropriate definition of α is ‘mean species diversity per subunit’ (where ‘diversity’ needs to be changed to ‘richness’ if the focus is on presence–absence data rather than abundance data; see below and Tuomisto 2010c).

Whittaker (1960) only considered a multiplicative partitioning of gamma diversity ($\gamma = \alpha \times \beta$). Ever since Lande (1996) introduced the additive partitioning ($\gamma = \alpha + \beta$), it has been debated which of the two is better (e.g., Baselga 2010; Jost 2010; Ricotta 2010; Veech and Crist 2010; Jurasinski and Koch 2011). In my opinion, this question has two different answers. Firstly, if the question is considered in terms of nomenclature, the answer is that only the components of the multiplicative partitioning should be called ‘alpha diversity’ and ‘beta diversity’. This is because Whittaker himself used the terms in this way, and as the components of the additive partitioning are different, they should be given other names. Secondly, if the question is considered in terms of the utility of the components in answering practical ecological questions, the answer is that both partitionings can be useful. Both are mathematically valid, but since their components have different mathematical and conceptual properties, they serve different purposes and are relevant in different situations (Tuomisto 2010a, c).

To make the distinction explicit, I have proposed the notation α_d and β_{Md} for the components of the multiplicative partitioning, and the notation α_t and β_{At} for the components of the additive partitioning (Tuomisto 2010a). Even more explicit notations would be ${}^qD_\gamma = {}^qD_\alpha \times {}^qD_\beta$ for the multiplicative partitioning (following Jost 2006,

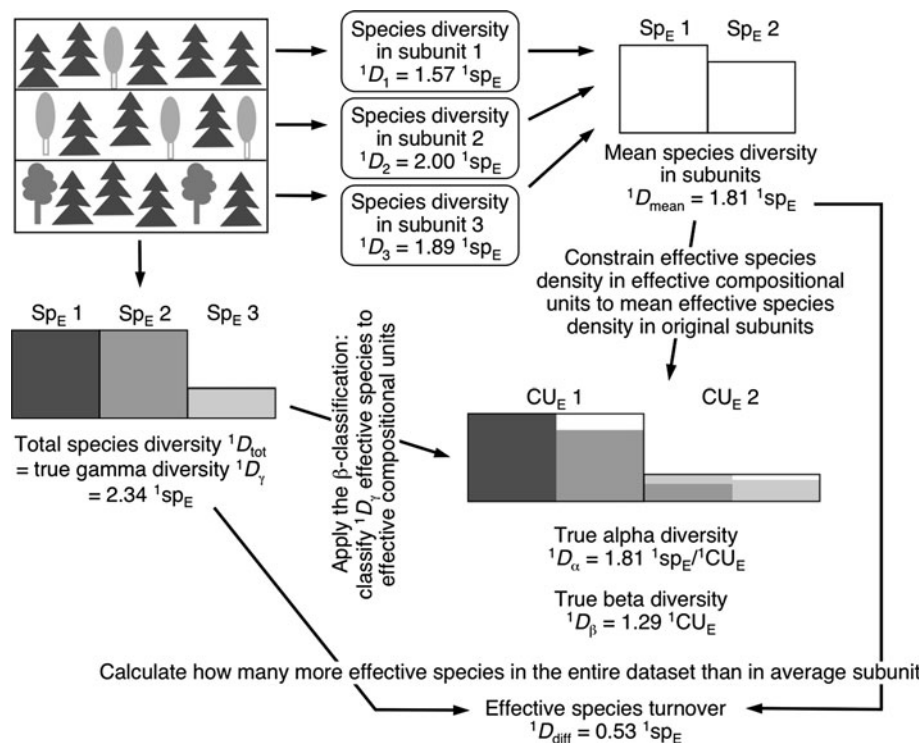


Fig. 2 Two different ways of partitioning the total species diversity of a dataset (*true gamma diversity*) into two components, given three subunits. The dataset is the same as in Fig. 1, but only true diversities of order one (which are based on the geometric mean of species proportional abundances) are shown for simplicity. Species diversity in each subunit j (1D_j) is calculated in the same way as species diversity in the entire dataset ($^1D_{\gamma} = ^1D_{\text{tot}}$; see Fig. 1). Multiplicative partitioning gives two conceptually and mathematically independent

components, namely the effective number of compositionally distinct units (*true beta diversity*), and the mean effective species density in those compositional units (*true alpha diversity*). Additive partitioning gives two components that represent the same concept as does true gamma diversity, namely species diversity. One of these components quantifies the mean within-subunit species diversity ($^1D_{\text{mean}}$), and the other ($^1D_{\text{diff}}$) quantifies the total number of effective species that differ (*turnover*) among all subunits

2007), and $^qD_{\text{tot}} = ^qD_{\text{mean}} + ^qD_{\text{diff}}$ for the additive partitioning (proposed here). Although $^qD_{\gamma} = ^qD_{\text{tot}}$, two different symbols are useful to emphasize that the multiplicative partitioning produces components that differ in which classification of entities they are based on, whereas the additive partitioning produces components that differ in which part of the dataset they refer to.

Gamma diversity $^qD_{\gamma}$ is the effective number of types corresponding to the gamma classification (which classifies the individuals that form the dataset into species; see Fig. 1; Tuomisto 2010a) and beta diversity $^qD_{\beta}$ is the effective number of types corresponding to the beta classification (which classifies the species of the dataset into compositional units; Fig. 2). Alpha diversity $^qD_{\alpha}$ is conceptually a density measure: it quantifies the mean density (or concentration) of effective species within the units obtained with the beta classification (Fig. 2). The total (effective) number of species in a dataset is obtained by multiplying the (effective) number of units in the dataset by the (effective) density of species per unit. Consequently, each one of the three terms in the multiplicative equation has a different measurement unit: effective species $^q\text{sp}_E$ for

gamma diversity, effective compositional unit $^q\text{CU}_E$ for beta diversity, and effective species per effective compositional unit $^q\text{sp}_E / ^q\text{CU}_E$ for alpha diversity (Tuomisto 2010a, c; note the addition of the superscript to indicate on which value of q the measure is based). I believe this interpretation is compatible with what earlier authors had in mind when arguing that the alpha and beta components of the multiplicative partitioning represent independent aspects of gamma diversity (Whittaker 1960, 1972; Routledge 1979; Jost 2006, 2007, 2010; Tuomisto 2010a, b, c). Analogously, the total sugar content of an apple (cf. γ) is a product of the number of weight units the apple contains (cf. β_{Md}) and the mean concentration of sugar per unit weight (cf. α_d).

In contrast, each term in the additive partitioning refers to the same kind of diversity, namely the diversity in relation to the gamma classification, and each term hence has the same measurement unit $^q\text{sp}_E$. The three terms differ in that each quantifies species diversity in a different part of the dataset. $^qD_{\text{tot}}$ (γ) is the total species diversity in the entire dataset. $^qD_{\text{mean}}$ (α) is the species diversity in an average subunit (i.e. mean species diversity in all the

subunits of the dataset). ${}^qD_{\text{diff}}(\beta_{\text{At}})$ is the species diversity in the rest of the dataset (i.e. the difference between the other two; Tuomisto 2010c). Analogously, the total sugar content of an apple (cf. γ) is the sum of the mean sugar content in a slice equaling one unit of weight (cf. α_t) and the sugar content in the rest of the apple (cf. β_{At}). All the terms in the additive equation (${}^qD_{\text{tot}}$, ${}^qD_{\text{mean}}$ and ${}^qD_{\text{diff}}$) could have γ as a subscript, because all of them quantify species diversity (i.e. diversity in relation to the gamma classification). However, to simplify the notation, it can be assumed that when the focal part of the dataset is explicitly specified, then the interest is always in the gamma classification and the subscript γ can be omitted. Similarly, when the focal part of the dataset is not specified, it can be assumed that the entire dataset is meant.

With presence–absence data, the additive partitioning can be written $S_{\text{tot}} = S_{\text{mean}} + S_{\text{diff}}$ when the focus is on Species richness (and the measurement unit is hence sp), or $R_{\text{tot}} = R_{\text{mean}} + R_{\text{diff}}$ when the focus is on Richness in general (and the measurement unit may be species but it may also be something else, such as genus, family or functional type). When the multiplicative partitioning is applied to presence–absence data, it is best written using the general form $R_{\gamma} = R_{\alpha} \times R_{\beta}$ because only gamma richness can actually be measured in units of species. Beta richness is invariably measured in compositional units CU, and alpha richness has a composite measurement unit such as sp/CU (note that Tuomisto 2010c used the notation based on S without realising that it can be confusing due to the strong association of S with the number of species in the ecological literature).

The beta component of the multiplicative partitioning equals true beta diversity, but the beta component of the additive partitioning corresponds to what I prefer to call species turnover (Fig. 2; Tuomisto 2010a). Other phenomena, such as entropies and probabilities, can also be partitioned multiplicatively and additively, and these components may be very useful when addressing some ecological questions. However, the components obtained then represent entropies and probabilities rather than true diversity, and they have to be interpreted accordingly.

When interpreting the results, it is important to take into account how a variable behaves when all species in a dataset are replicated such that each species gives rise to a new species of the same absolute abundance as the original one. True gamma diversity (${}^qD_{\gamma} = {}^qD_{\text{tot}}$) and true alpha diversity (${}^qD_{\alpha}$) follow the replication principle: their values double. This is also the case with both components of the additive partitioning (${}^qD_{\text{mean}}$ and ${}^qD_{\text{diff}}$). True beta diversity (${}^qD_{\beta}$), in contrast, is replication invariant: its value does not change when species are replicated. Entropies and probabilities do not follow the replication principle, but they are not replication invariant either. Interpreting

components of an entropy as if they were components of true diversity can therefore lead to seriously incorrect conclusions (Jost 2007, 2010; Tuomisto 2010a).

The meaning of ‘species turnover’

Like ‘diversity’, ‘species turnover’ is a tricky term that has been used to refer to various phenomena. Whittaker (1972: pp. 214, 232–233) equated ‘species turnover’ with ‘compositional change’ and considered it as one kind of beta diversity. His focus was on measuring species turnover along environmental gradients, and several researchers have since then argued that ‘species turnover’ should only be used to refer to compositional change along an explicit external gradient (Vellend 2001; Moreno and Rodríguez 2010; Anderson et al. 2011; Jurasinski and Koch 2011). In my view, a more logical terminology results if both ‘compositional change’ and ‘species turnover’ themselves just refer to (specific kinds of) difference in species composition, and additional specifiers are used to indicate if this is quantified between two sampling units, among many sampling units, or along an environmental or spatial gradient (Tuomisto 2010b).

If the term ‘species turnover’ itself already implies that the compositional change is measured along an external gradient, a different term would be needed to refer to compositional change among sampling units that are not explicitly related to any environmental gradient. Vellend (2001) suggested that ‘beta diversity’ be used for this purpose, but doing so leads to terminological inconsistency, as explained above. Anderson et al. (2011) proposed the term ‘variation’ instead, but this is a very vague term. In addition, their use of the two terms is not entirely logical: most of their analyses of variation still concern external gradients, just as do their analyses of turnover. The main difference seems to be that turnover is measured for pairs of sites, whereas variation is mostly (but not exclusively) measured for larger groups of sites. This distinction seems to imply that Anderson et al. consider the ‘beta turnover’ measure of Wilson and Shmida (1984) a measure of variation (category V1 of Anderson et al. 2011) rather than a measure of turnover, even though its explicit purpose is to quantify species turnover along a gradient.

Compositional change can be quantified with any of numerous dissimilarity indices, only some of which can be derived from the additive partitioning of gamma diversity (or of gamma richness if the focus is on presence–absence data; Tuomisto 2010a, c). To clarify the terminology, I propose that the term ‘species turnover’ be reserved to the subset of dissimilarity (compositional change) measures that can be expressed as a function of γ and α_t (Tuomisto 2010a). These measures are absolute species turnover = $\gamma - \alpha_t$,

Whittaker's species turnover = $(\gamma - \alpha_t)/\alpha_t = \gamma/\alpha_t - 1$, and proportional species turnover = $(\gamma - \alpha_t)/\gamma = 1 - \alpha_t/\gamma$. When calculated between two sampling units using presence–absence data, Whittaker's species turnover equals the one-complement of the Sørensen index, and proportional species turnover ranged to the interval [0, 1] equals the one-complement of the Jaccard index. Most popular dissimilarity measures are not functions of α_t and γ (e.g., the Bray–Curtis, chord, Hellinger and chi-squared distances).

In measures based on presence–absence data, γ and α_t are counts of the actual named species (R_{tot} and R_{mean} , respectively), whereas in measures based on abundance data, γ and α_t are counts of effective species (${}^qD_{\text{tot}}$ and ${}^qD_{\text{mean}}$, respectively). Figure 2 only shows the latter, but a figure based on the former would be similar except that all variables would represent richness rather than diversity. The conceptual difference between richness and diversity is evident in that the values of each are taken from a different phase of the process shown in Fig. 1 (each phase corresponding to a different wall of pigeonholes in the analogy of Tuomisto 2010c). To separate between these conceptually different measures, the turnover corresponding to presence–absence data can be called 'actual species turnover' and the turnover corresponding to abundance data can be called 'effective species turnover' (Tuomisto 2010c). Each species (effective or actual) that changes to another one when one moves from one compositional unit (effective or actual) to another equals one species turned over.

Analysing beta diversity

Because such a wide range of different phenomena have been called beta diversity, most ecological studies that have claimed to analyze beta diversity have actually not addressed true beta diversity at all. For example, the regression analyses that are based on CCA and RDA (Legendre et al. 2005; Anderson et al. 2011) analyze the species by sites raw data matrix in order to explain variance in species abundances (level-2 analyses sensu Tuomisto and Ruokolainen 2006, 2008), and true beta diversity does not enter the calculations at any stage. Even the distance-based methods (Mantel test and its derivatives; level-3 analyses) do not address true beta diversity, because true beta diversity is not a dissimilarity measure. Instead, these methods address species turnover or other measures of compositional dissimilarity (Tuomisto 2010b).

In the roadmap of Anderson et al. (2011), all mission statements supposedly concern beta diversity. However, it remains ambiguous which definition of the term is actually meant in each mission statement, and which questions related to that definition are addressed in each of the

analytical methods that are mentioned (see also Jurasinski and Koch 2011; Moreno and Rodríguez 2011). As a result, the roadmap gives little guidance to ecologists who wish to avoid confusing the different beta diversities, or who seek advice on appropriate methods when addressing questions related to a particular definition of beta diversity.

In terms of data analysis, Anderson et al. (2011) mostly seem to address 'variation' using the raw data approach (level-2 methods) and 'turnover' using the distance approach (level-3 methods). This, in turn, implies that 'variation' is thought of as the variation to be explained in the analysis, whereas 'turnover' is thought of as the response variable of the analysis. In other words, the distinction between 'variation' and 'turnover' is not based on what phenomena they represent but on how they are treated in data analysis. Both kinds of analyses may or may not involve environmental gradients, which leads to a logical inconsistency: Anderson et al. (2011) had earlier defined that 'turnover' is measured along an explicit external gradient whereas 'variation' is not.

Conclusions

Applying the term beta diversity to several non-diversity phenomena causes confusion, incorrect ecological inferences and unwarranted comparisons among studies, just as would applying the term *Malus domestica* to several unrelated plants. Biologists manage quite well in dealing with nomenclature problems that arise from the sloppy use of common names that refer to taxa, such as (true) bugs. Why could we not achieve the same with common names that refer to concepts, such as (true) diversity? Although the term 'diversity' (especially 'beta diversity') has traditionally been used to refer to conceptually different phenomena, Hill (1973) laid the foundation for a consistent nomenclature that has been built on especially by Jost (2006, 2007). Inspired by their work, I have proposed a framework that includes unique names for most of the phenomena that have been called beta diversity in the ecological literature (Tuomisto 2010a, b, c). No doubt finetuning is needed before the terminology becomes fully comprehensive, but for the most common purposes, a consistent terminology for diversity-related concepts is already available. The question is whether or not we choose to use it, which has implications for our capacity to understand diversity issues and to communicate that understanding to others.

Acknowledgments I thank Root Gorelick, Gerald Jurasinski, Claudia Moreno, Samuel M. Scheiner, Marti J. Anderson and Kalle Ruokolainen for fruitful discussions that helped focus the present paper.

References

- Anderson MJ, Crist TO, Chase JM, Vellend M, Inouye BD, Freestone AL et al (2011) Navigating the multiple meanings of β diversity: a roadmap for the practicing ecologist. *Ecol Lett* 14:19–28
- Baselga A (2010) Multiplicative partition of true diversity yields independent alpha and beta components; additive partition does not. *Ecology* 91:1974–1981
- Gorelick R (2011) Commentary: do we have a consistent terminology for species diversity? The fallacy of true diversity. *Oecologia*. doi:[10.1007/s00442-011-2124-8](https://doi.org/10.1007/s00442-011-2124-8)
- Hill MO (1973) Diversity and evenness: a unifying notation and its consequences. *Ecology* 54:427–432
- Hoffmann S, Hoffmann A (2008) Is there a “true” diversity? *Ecol Econ* 65:213–215
- Hurlbert SH (1971) The nonconcept of species diversity: a critique and alternative parameters. *Ecology* 52:577–586
- Jost L (2006) Entropy and diversity. *Oikos* 113:363–375
- Jost L (2007) Partitioning diversity into independent alpha and beta components. *Ecology* 88:2427–2439
- Jost L (2009) Mismeasuring biological diversity: response to Hoffmann and Hoffmann (2008). *Ecol Econ* 68:925–928
- Jost L (2010) Independence of alpha and beta diversities. *Ecology* 91:1969–1974
- Jurasinski G, Koch M (2011) Commentary: do we have a consistent terminology for species diversity? We are on the way. *Oecologia*. doi:[10.1007/s00442-011-2126-6](https://doi.org/10.1007/s00442-011-2126-6)
- Jurasinski G, Retzer V, Beierkuhnlein C (2009) Inventory, differentiation, and proportional diversity: a consistent terminology for quantifying species diversity. *Oecologia* 159:15–26
- Lande R (1996) Statistics and partitioning of species diversity, and similarity among multiple communities. *Oikos* 76:5–13
- Legendre P, Borcard D, Peres-Neto PR (2005) Analyzing beta diversity: partitioning the spatial variation of community composition data. *Ecol Monogr* 75:435–450
- Moreno CE, Rodríguez P (2010) A consistent terminology for quantifying species diversity? *Oecologia* 163:282–297
- Moreno CE, Rodríguez P (2011) Commentary: do we have a consistent terminology for species diversity? Back to basics and toward a unifying framework. *Oecologia*. doi:[10.1007/s00442-011-2125-7](https://doi.org/10.1007/s00442-011-2125-7)
- Ricotta C (2010) On beta diversity decomposition: trouble shared is not trouble halved. *Ecology* 91:1981–1983
- Routledge RD (1979) Diversity indices: which ones are admissible? *J Theor Biol* 76:503–515
- Tuomisto H (2010a) A diversity of beta diversities: straightening up a concept gone awry. Part 1. Defining beta diversity as a function of alpha and gamma diversity. *Ecography* 33:2–22
- Tuomisto H (2010b) A diversity of beta diversities: straightening up a concept gone awry. Part 2. Quantifying beta diversity and related phenomena. *Ecography* 33:23–45
- Tuomisto H (2010c) A consistent terminology for quantifying species diversity? Yes, it does exist. *Oecologia* 164:853–860
- Tuomisto H, Ruokolainen K (2006) Analyzing or explaining beta diversity? Understanding the targets of different methods of analysis. *Ecology* 87:2697–2708
- Tuomisto H, Ruokolainen K (2008) Analyzing or explaining beta diversity? Reply. *Ecology* 89:3244–3256
- Veech JA, Crist TO (2010) Toward a unified view of diversity partitioning. *Ecology* 91:1988–1992
- Vellend M (2001) Do commonly used indices of β -diversity measure species turnover? *J Veg Sci* 12:545–552
- Whittaker RH (1960) Vegetation of the Siskiyou Mountains, Oregon and California. *Ecol Monogr* 30:279–338
- Whittaker RH (1972) Evolution and measurement of species diversity. *Taxon* 21:213–251
- Wilson MV, Shmida A (1984) Measuring beta diversity with presence–absence data. *J Ecol* 72:1055–1064